

M. Jäggi · R. Siegwolf · M. Genenger ·
D. Hallenbarter · I. Brunner · J. Fuhrer

Wood ash treatment affects seasonal N fluctuations in needles of adult *Picea abies* trees: a ^{15}N -tracer study

Received: 19 December 2002 / Accepted: 20 June 2003 / Published online: 22 July 2003
© Springer-Verlag 2003

Abstract A ^{15}N -tracer experiment was carried out in a stand of adult spruce trees [*Picea abies* (L.) Karst.] located on the Swiss Plateau in order to investigate the effects of wood ash treatment on seasonal nitrogen fluctuations in fine roots and needles. Treatments included irrigation (W), liquid fertilization (LF) and wood ash (A) application. ^{15}N fluctuation in fine roots and current to 3-year-old needles was studied after one ^{15}N pulse for 2 consecutive years (1999, 2000). ^{15}N tracer was rapidly incorporated into the fine roots of adult trees, and $\delta^{15}\text{N}$ values reached similar levels in all treatments 2 months after the pulse. In the needles, the largest increase in $\delta^{15}\text{N}$ was observed in those of the current year. Following the initial peak during spring growth, $\delta^{15}\text{N}$ values in needles of control trees showed an oscillating pattern through the season. This oscillation is attributed to the increased use of internal N sources, as soon as the roots can no longer meet the increased N demand during the sprouting phase. However, W-, LF- and A-treated trees no longer showed the oscillation in $\delta^{15}\text{N}$. Additional water (W and LF) as well as fertilizer (A and LF) may have induced shifts in the microbial flora, thus increasing the unlabelled N

release from the soil. The strongest dampening was observed for the A treatment, indicating sufficient N availability from the soil, and making intensive use of the internal N sources unnecessary. Treatment with wood ash thus resulted in a similar fertilizer response to liquid fertilization.

Keywords Liquid fertilization · Needle biomass · Nitrogen content · Variation in $\delta^{15}\text{N}$ · Wood ash

Introduction

In the context of renewable energy sources, an increase in the demand for wood to substitute fossil fuels can be expected. The removal of slash means a several-fold increase in the harvest of nutrients compared to conventional forestry (Nohrstedt 2001). Without compensatory measures, nutrient depletion within forest ecosystems may result (Ingerslev et al. 2001), reducing wood biomass production in the long term. Atmospheric nitrogen (N) deposition (Wellburn 1998; Ammann et al. 1999; Siegwolf et al. 2001) or conventional fertilizer treatments (Ingstad et al. 1981; Linder 1987) could be regarded as compensatory measures. Moreover, wood ash recycling by returning wood ash produced from wood burning (Hagerberg and Wallander 2002) could be a suitable alternative measure even though it is an N-free fertilizer. Wood ash application to coniferous forests, as well as other fertilizer treatments, has been studied frequently in Nordic Countries to improve wood growth (Ingerslev et al. 2001; Nohrstedt 2001; Saarsalmi and Mälkönen 2001). For temperate forests in Switzerland, however, such studies are still lacking, even though an excess of wood ash has been reported in Switzerland (Hallenbarter et al. 2002).

Recycling of wood ash has become an important issue (Saarsalmi and Mälkönen 2001). However, wood ash may contain potentially hazardous compounds, e.g. heavy metals and radionuclides (Nohrstedt 2001), causing unwanted soil pollution in forests (Zhan et al. 1996).

M. Jäggi · R. Siegwolf (✉)
Paul Scherrer Institut,
5232 Villigen PSI, Switzerland
e-mail: rolf.siegwolf@psi.ch
Tel.: +41 56 310 27 86
Fax: +41 56 310 45 25

M. Genenger · D. Hallenbarter · I. Brunner
Swiss Federal Institute for Forest,
Snow and Landscape Research (WSL),
Zürcherstrasse 111, 8903 Birmensdorf, Switzerland

J. Fuhrer
Swiss Federal Research Station for Agroecology
and Agriculture FAL Reckenholz,
8046 Zürich, Switzerland

Present address:

M. Jäggi, Swiss Federal Research Station for Agroecology
and Agriculture FAL Reckenholz,
8046 Zürich, Switzerland

The toxic effect of wood ash on forest soils can be reduced, by (1) using untreated wood for burning, (2) optimizing the temperature prevailing during the burning process (Etiegni and Campbell 1991), and (3) restricting the applied doses to a maximum of 3 ton ha⁻¹ (Nohrstedt 2001).

In general, wood ash is applied to forest ecosystems to counteract natural or anthropogenic soil acidification (Ingerslev et al. 2001). Applied to forest soils, this treatment can cause an increase in pH and improve the supply of base cations (Fritze et al. 1994; Bramryd and Fransman 1995; Mälikönen et al. 1999). In the case of N-rich soils (low C/N ratio), this treatment can increase tree growth, mineralization and leaching of N in soils, whereas ash application on N-poor soils (high C/N ratio) can cause N to be immobilized and tree growth to be decreased (Ingerslev et al. 2001). The effects of wood ash application on nutrient contents in conifer needles range between (1) no change in nutrient contents (McDonald et al. 1994), (2) a decrease in nitrogen content (N_{cont}) (Shepard 1997), or even (3) an increase in the amounts of foliar elements in closed stands (Egnell et al. 1998). A poor N supply in wood ash treatments could also increase nitrogen use efficiency (NUE), resulting in increased tree internal cycling of N (Birk and Vitousek 1986). Therefore, tree internal nutrient translocation to young leaves or needles may be important (Nambiar and Fife 1991). One way to measure the amount of remobilized N required to sustain growth is to apply ¹⁵N to the soil before bud burst and then calculate the amount of N in leaves by the recovery of ¹⁵N originating from the soil (Millard 1994). Such experiments with highly ¹⁵N enriched N compounds as tracers have been used to observe the movement of N in coniferous stands, and to identify the effect of fertilization (Mead and Pritchett 1975a, 1975b; Nommik 1990; Schleppi et al. 1999). As far as we know, however, the ¹⁵N-tracer technique has not yet been used to study effects of wood ash application.

The aim of the overall study was to investigate the potential effects on vegetation caused by wood ash recycling compared to steady-state fertilization (Ingestad et al. 1981) in a mature forest in Switzerland. This site was regarded as N saturated based on Gundersen (1998), since high nitrate concentration in the soil solution was observed in the present study (Genenger et al. 2003b). Such conditions may favour increased mineralization and N release from the soil by wood ash amendment. Hallenbarter et al. (2002) observed that wood ash and liquid fertilization caused no shifts in nutrient contents and ratios in needles based on yearly data. However, tree

growth increased following both treatments, as reflected mainly by a trend in increased shoot and needle growth (Hallenbarter et al. 2002). Treatment influences on the seasonal N dynamics in spruce needles are as yet lacking within this project.

This study presents data on the seasonal course of N fluctuations in fine roots and 1- to 3-year-old needles, assessed with the help of a single ¹⁵N pulse-labelling experiment. We tested the hypothesis that the internal cycling of N, in times of increased needle growth (spring) or N storage (autumn), is reduced due to the wood ash treatment and liquid fertilization. Therefore, we assumed the fertilization effect of wood ash to be less strong than the liquid fertilization on the seasonal course of N oscillation in fine roots and spruce needles.

Materials and methods

Field site

The experiment was carried out at the forest site "Schladholz" (47°30'34"N, 08°20'50"E, 464 m above sea level) located about 25 km NW of Zurich (Switzerland). After a clear cut in 1930, the forest was replanted with Norway spruce [*Picea abies* (L.) Karst.] and beech trees (*Fagus sylvatica* L.). The age of the 16 trees sampled in this experiment ranged between 43 and 62 years; thus they are considered adult trees. Detailed description of tree age, height and diameter are given as average values per treatment in Table 1. The site covers an area of about 8,000 m². We used climatological data from 1990 to 2000 of the nearby Buchs-Suhr MeteoSwiss station (47°23'N, 08°5'E; 387 m above sea level). Annual mean air temperature is 9.7°C and precipitation is 1,064 mm. The precipitation amount during the growing season (May–September) averages about 537 mm. The soil is an acidic brown forest soil. More detailed information is given in Bundt et al. (2001). The most frequent species of the understory vegetation are *Rubus fruticosus* s.l., *Oxalis acetosella* and *Rubus idaeus* (E. Thürig, personal communication).

Treatments

Four different treatments were applied to four plots (16 plots in total) with a surface area of about 500 m² (for more details see Genenger et al. 2003a): control plots without any treatment (C), irrigated plots receiving an additional 197 mm in 1998, 194 mm in 1999 and 202 mm in 2000 of precipitation (7.6 kg N ha⁻¹ year⁻¹), corresponding to about one-third of the average ambient precipitation amount of 537 mm (W), liquid-fertilized plots (LF), treated with 72 kg N ha⁻¹, 93 kg N ha⁻¹ and 99 kg N ha⁻¹ in 1998, 1999 and 2000 (applied in equivalent amounts of water as in W), and plots supplied twice with dry wood ash spread by hand at 4,000 kg ha⁻¹ year⁻¹ (1998 and 1999) (A). The elemental concentration of liquid fertilizer (according to Ingestad 1981) and wood ash are described in detail in Table 2. Irrigation and liquid fertilization were maintained during the growing season (May–September) in

Table 1 Averaged values for spruce tree age, height and diameter, separated by the different treatments applied in this study. Means ± SE in all parameters are calculated for n=4

Treatment	Tree age (year)	Tree height (m)	Tree diameter at 1.3 m height (m)
Wood ash	50±8	31.90±1.93	0.40±0.06
Control	56±8	30.58±3.49	0.40±0.06
Liquid fertilization	50±5	32.93±1.25	0.36±0.06
Irrigation	57±3	31.35±2.14	0.41±0.06

Table 2 Chemical composition of the liquid-fertilizer and wood-ash treatment, applied in this study for the years 1998–2000

Element	Liquid-fertilizer (g m ⁻² year ⁻¹)			Wood-ash (g m ⁻² year ⁻¹)	
	1998	1999	2000	1998	1999
N	7.20	9.30	9.9	1.92×10 ⁻⁵	2.58×10 ⁻⁵
P	1.32	1.71	1.82	6.28	6.26
K	6.32	8.16	8.69	21.23	25.15
Ca	0.48	0.62	0.66	116.31	112.57
S	0.48	0.62	0.66	2.75	2.49
Mg	0.80	1.03	1.10	7.76	7.46
Mn	4.16×10 ⁻³	5.37×10 ⁻³	5.72×10 ⁻³	1.34	2.39
Fe	6.76×10 ⁻³	8.73×10 ⁻³	9.30×10 ⁻³	1.83	2.08
Zn	0.60×10 ⁻³	0.78×10 ⁻³	0.83×10 ⁻³	0.63×10 ⁻¹	0.67×10 ⁻¹
Cu	0.60×10 ⁻³	0.78×10 ⁻³	0.83×10 ⁻³	40.96×10 ⁻³	50.48×10 ⁻³
B	2.04×10 ⁻³	2.64×10 ⁻³	2.81×10 ⁻³	—	—
Mo	0.76×10 ⁻⁴	0.98×10 ⁻⁴	1.05×10 ⁻⁴	4.80×10 ⁻⁴	4.80×10 ⁻⁴
Cd	—	—	—	1.44×10 ⁻³	1.48×10 ⁻³
Co	—	—	—	1.52×10 ⁻³	1.88×10 ⁻³
Pb	—	—	—	1.19×10 ⁻²	1.22×10 ⁻²
C	—	—	—	4.65×10 ⁻³	1.65×10 ⁻³

1998–2000. The liquid fertilizer was dissolved in 800, 1,000 and 1,000 l of water (Hauert, HBG Düngervertrieb, 3257 Grossaffoltern, Switzerland) for 1998, 1999 and 2000, respectively, and equally distributed on the LF plots by means of a sprinkler system. Water was pumped from a nearby stream to the irrigated and liquid-fertilized plots and applied nightly (9 p.m. to 2.30 a.m.) by means of a sprinkler system. A heavy storm (“Lothar”) on 26 December 1999 caused considerable damage and reduced the number of experimental trees to 12 during the third year (C, $n=3$; W, $n=3$; A, $n=4$; LF, $n=2$).

¹⁵N labelling and analysis

According to Buchmann et al. 1995, we adopted the calculation of the natural ¹⁵N pool as the sum of N in the soil and in plant biomass, multiplied by the natural fraction of ¹⁵N (0.003663), where the ¹⁵N addition was calculated as 5% of the total natural ¹⁵N pool. For labelling, the added ammonium-nitrate was highly ¹⁵N enriched (98%). Thus only a very small amount of tracer provided a strong signal in the needles, without causing any fertilizing effect, although the soil N_{cont} in our plots (Bundt et al. 2001) was higher than reported by Buchman et al (1995). In April 1999, 16 trees (four treatments with four replicates each) were supplied with 58.4 mg N m⁻² in the form of the double-labelled ¹⁵NH₄¹⁵NO₃.

The tracer was evenly distributed over a circular area of 30 m² (diameter of 6 m) around each experimental tree. At the time of application, understory vegetation was scarcely developed, however, spreading the tracer on vegetative parts could not be completely avoided. In order to strictly avoid spreading of tracer to adjacent areas, disposable plastic shoes were worn and discarded after each plot was labelled.

Samples were taken four times in 1998 (January, May, August and October), six times in 1999 (January, April, May, June, July and October) and four times in 2000 (January, May, July and October), from four different needle age classes (current, 1-year, 2-year and 3-year-old) in the upper third of the sun-exposed crown. Samples were oven-dried at 65°C and ground to a fine powder with a steel ball mill (Mixer Mill, Retsch MM2000, Germany). Total N concentration and the isotopic signature of each sample were measured with an Elemental Analyzer (EA-1110, Carlo Erba, Italy) connected to a continuous flow mass spectrometer (DELTA-S Finnigan MAT, Germany). The isotopic signatures are expressed in the delta notation $\delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1,000$ (‰), relative to the international standards (N₂ in air).

Fine roots (diameter <2 mm) were sampled before (April 1999) and 1, 3, and 7 days (Genenger et al. 2003a) and 1, 2, 6 and 13 months after the tracer application. Three root samples per tree were collected at 5 cm below ground within 1 m from the trunk,

rinsed with distilled water, frozen in liquid N and then stored at -80°C. Finally, the fine roots were freeze-dried for 48 h, ground to a fine powder and analysed as mentioned above.

The dry weight of current-year needles in winter (1997, 1998, 1999 and 2000) was estimated using 100 needles from each experimental tree. The needles were then ground to a fine powder and analysed as described above. Tree cores were sampled in winter 1999 and 2000 and a detailed description is given in Jäggi et al. (2002).

¹⁵N recovery in needles

N_{cont} of current-year needles in winter 1999 and 2000 was calculated by multiplying the N concentration with the corresponding biomass of 100 needles. According to Buchmann et al. (1996), the ¹⁵N enrichment, measured as δ units, is calculated as ¹⁵N frequency in atom%: $\text{atom}\% = F_{\text{sample}} \times 100$. The fractional abundance F_{sample} is thereby defined as $F_{\text{sample}} = {}^{15}\text{N} / ({}^{15}\text{N} + {}^{14}\text{N}) = {}^{15}\text{N} : {}^{14}\text{N}_{\text{sample}} / ({}^{15}\text{N} : {}^{14}\text{N}_{\text{sample}} + 1)$.

To account for the natural abundance in current-year needles of the 16 investigated trees, data of winter 1998 (after 1 year of treatment application) was chosen for the still unlabelled trees (atom%_{unlab}), whereas the ¹⁵N recovery (¹⁵N_{recov}) of the labelled trees (atom%_{lab}) was calculated for current-year needles in winter 1999 and 2000 (after the second and third year of treatment application). The biomass and N_{cont} of unlabelled and labelled trees were assumed to be equal in each year: ${}^{15}\text{N} = (\text{atom}\%_{\text{lab}} - \text{atom}\%_{\text{unlab}}) \times \text{N}_{\text{cont}}$.

The total recovery of ¹⁵N was thus calculated in milligrams per 100 needles and averaged per treatment (±SD), 9 and 21 months after treatment application.

Statistical analysis

Treatment effects on $\delta^{15}\text{N}$ values, needle biomass, N_{cont}, ¹⁵N recovery and tree-ring width in the field experiment were tested with a one-way ANOVA. All statistical analyses were carried out with the program StatView (SAS Institute).

Results

Seasonal ^{15}N dynamics

The development of $\delta^{15}\text{N}$ signals in fine roots showed that maximum mean $\delta^{15}\text{N}$ values between 400‰ and 525‰ were reached in irrigated adult trees after 1 month (Fig. 1). The increase in $\delta^{15}\text{N}$ in fine roots of controls or trees treated with wood ash or liquid fertilizer was slower, but the values reached 2 months after the tracer application were about 400‰ in all treatments. Thereafter the $\delta^{15}\text{N}$ values decreased steadily to about 300‰ 13 months after tracer application. The variability within individual treatments was considerable, as expressed by the standard error given in Fig. 1.

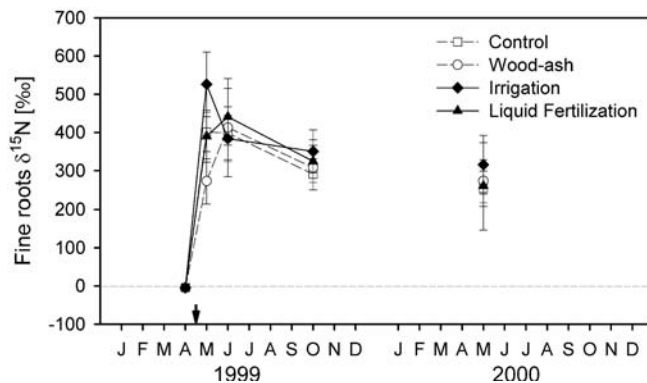
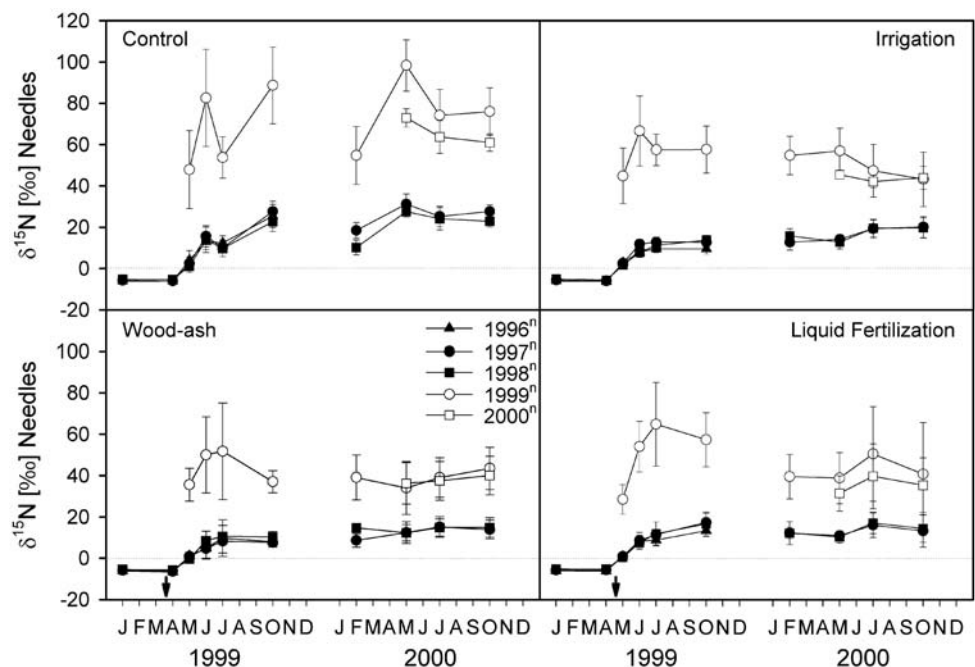


Fig. 1 Uptake of the ^{15}N tracer in fine roots, split by the different treatments. The dashed lines indicate the dry treatments (wood ash and control) and the solid lines stand for the wet treatments (liquid fertilization and irrigation)

Fig. 2 The ^{15}N uptake of the needles developed in the years 1996ⁿ through 2000ⁿ, for the two sampling years 1999 and 2000, are separated by the four different treatments. The two arrows between April and May 1999 indicate the application time of the ^{15}N tracer. The superscript letter (n) after the number of a year shows the year in which this needle was newly developed. One-way ANOVA did not reveal statistical significance at the 5% probability level for 1999ⁿ in all four treatments



The increase in $\delta^{15}\text{N}$ values in needles was slow, compared to the rapid ^{15}N uptake in fine roots during the first month after tracer application. In the recent needles in 1999 highest mean levels of the tracer were observed after 2 months in C and W trees, and after 3 months in A and LF trees (Fig. 2). The maximum mean value of 83‰ was found in the C trees. The two irrigated treatments showed similar maxima of about 65‰ (LF) and 67‰ (W). A-treated trees showed the lowest value of 52‰. The youngest needle age classes (1999ⁿ, 2000ⁿ) showed the highest mean ^{15}N signals; differences in $\delta^{15}\text{N}$ between the older needle age classes were small.

The development of $\delta^{15}\text{N}$ values in 1999ⁿ needles, i.e. in needles newly developed in the year 1999, for C trees showed an oscillating pattern (Fig. 2). After the maximum mean values in June (1999), $\delta^{15}\text{N}$ dropped by more than 20‰. In October, $\delta^{15}\text{N}$ values increased again to levels similar to those in June. A similar pattern was observed in 2000, indicating that $\delta^{15}\text{N}$ values were generally high in spring and autumn, but lower in summer and winter. Similar fluctuations in $\delta^{15}\text{N}$ occurred in 3- to 1-year-old needles (1996ⁿ through 1998ⁿ, i.e. newly developed in these years). For all other treatments, fluctuations in $\delta^{15}\text{N}$ were small, yet fewest for the A treatment, and maximum mean values in 1999ⁿ needles occurred in June/July and followed a general decline afterwards. The values for recent needles 2000ⁿ were similar to those in 1999ⁿ needles. For control trees and trees treated with liquid fertilizer, a more pronounced difference between 1999ⁿ and 2000ⁿ needles was observed, as compared to the irrigated and wood ash treated trees. In comparison, the average natural abundance in $\delta^{15}\text{N}$ values in 1998 was negative and decreased slightly with the needle age (−4.8‰ in current year needles to −6.0‰ in 3-year-old needles, data not shown).

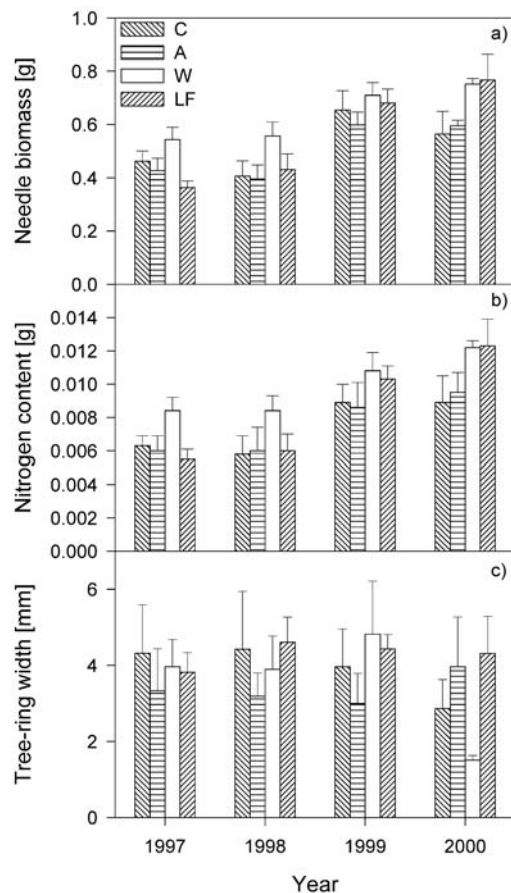


Fig. 3 Biomass (a) and nitrogen content (b) of 100 current-year needles in winter and tree-ring width (c), separated by the treatments control (C), wood ash (A), irrigation (W) and liquid fertilization (LF) for the years 1997–2000. ^{15}N pulse labelling was added before the 1999 data in this graph. Bars denote means of $n=4$, except for the year 2000, where $n=2-4 \pm \text{SE}$. One-way ANOVA did not reveal statistical significance at the 5% probability level, testing treatment effects in a–c

Biomass, N_{cont} of recent needles, and tree-ring width

One-way ANOVA revealed no significant effects of the treatments on needle biomass, N_{cont} and tree-ring width. However, significant differences occurred between years (except for the tree-ring width). Most pronounced is the increase in biomass and N_{cont} between the years 1998 and 1999, irrespective of the treatments (Fig. 3A, B). There is a trend towards constantly increasing biomass and N_{cont} values in needles of the LF treatment (Fig. 3A, B).

^{15}N recovery

The averaged total ^{15}N recovery per 100 current-year needles' N amount for all sample trees was $19.17\% \pm 7.89$ and $16.95\% \pm 5.34$, 9 and 21 months after tracer application, respectively. We found no significant treatment effects, however, if separated by treatments for the second experimental year (1999), the percentage of ^{15}N to total N

Table 3 ^{15}N recovery (mg) per 100 current-year needles 9 and 21 months after tracer application, separated by the different treatments. Means are presented for $n=4$ (1999) and $n=2-4$ (2000) \pm SD. There was no significant treatment effect on the 5% probability level (one-way ANOVA)

Treatment				
Year	Control	Wood ash	Irrigation	Liquid fertilization
1999	1.78 ± 0.49	1.25 ± 0.41	2.26 ± 0.49	1.63 ± 0.59
2000	1.85 ± 0.20	1.29 ± 0.28	2.09 ± 0.29	1.65 ± 0.70

is similar in C and W needles ($21.78\% \pm 10.37$ and $21.74\% \pm 6.85$), but lower in A and LF needles ($16.20\% \pm 8.20$ and $16.24\% \pm 6.75$). The absolute ^{15}N amounts showed similar values for C and LF needles, and higher values in W needles compared to C (Table 3). The A needles, however, showed the lowest ^{15}N amounts, yet similar N_{cont} and biomass as the C needles.

Discussion

Adult trees rapidly take up the ^{15}N tracer applied. Yet, since forest ecosystems contain a large N pool in the soil and in trees (Buchmann 1993), the tracer is diluted leading to lower $\delta^{15}\text{N}$ signals in fine roots and needles as compared to the original value of the tracer. The current foliage in adult spruce trees showed the maximum mean $\delta^{15}\text{N}$ signatures 2–3 months after the tracer application, whereas Buchmann et al. (1995) reported significant ^{15}N enrichment 11 days after tracer application in 1-year-old needles of field-grown 15-year-old spruce trees. The difference in height and age of the trees might account for the time lag in ^{15}N tracer uptake between roots and needles observed in this study. This could explain the delayed appearance of the ^{15}N signal in the needles of adult trees. The strongest $\delta^{15}\text{N}$ signal is found in the current-year spruce needles, indicating the high N demand of the newly forming foliage (Nambiar and Bowen 1986). No difference in $\delta^{15}\text{N}$ between the oldest three needle age classes in the adult trees was observed, which is in good agreement with the findings for a 250-year-old spruce tree stand (Schleppi et al. 1999).

Irrespective of the treatments, $\delta^{15}\text{N}$ remained fairly steady in fine roots after the initial rapid uptake with a decreasing tendency after 2 months. In non-irrigated trees (C and A) the initial ^{15}N tracer tended to be less rapidly absorbed than in trees receiving additional irrigation (W and LF). Genenger et al. (2003a) assumed this to be due to an improved N uptake capacity of the previous year in response to the treatments. In needles of the C and W trees, however, the maximum mean $\delta^{15}\text{N}$ values were reached 1 month earlier than in fertilized trees (A and LF). For the LF treatment, this could be explained by a dilution effect of tracer ^{15}N with non-labelled N from the soil. This indicates, that the wood ash treatment induced mineralization and thus increased the N availability from the soil (Ingerslev et al. 2001).

Under natural conditions, reflected by the oscillating ^{15}N pattern in C needles (Fig. 2; see also Buchmann et al. 1995), during periods of increased N demand and reduced external N supply (spring and autumn), internal sources become essential (Millard 1996; Gessler et al. 1998; Rennenberg et al. 1998). Such internal N sources can be (1) previous-year needles (Nambiar and Bowen 1986; Millard and Proe 1992), (2) wood and bark storage proteins (Roberts et al. 1991), or (3) N from senescing roots (Ferrier and Alexander 1991). In contrast to control trees, $\delta^{15}\text{N}$ in needles of the trees subject to LF and W treatment showed lower maximum mean values and less of a seasonal oscillation. The additional water in the W and LF treatment can lead to shifts in microbial populations, change the soil structure and pore volume, thereby affecting N transformation processes (Ruppel and Makswitat 1999). Likely, these effects on the soil microbial flora affect the N supply to the roots, which was shown for ammonium (Gessler et al. 1998; Rennenberg et al. 1998) and thus eliminate the oscillating $\delta^{15}\text{N}$ pattern in W and LF needles.

The strongest dampening effect on this oscillating ^{15}N pattern was observed in the A-treated needles, where additional water supply is lacking. This strongly suggests that the increase in pH observed (Genenger et al. 2003b) changed the mineralization in the soil (Fritze et al. 1994; Shepard 1997; Mäkönen et al. 1999) and thus the N availability for the trees (Shepard 1997; Ingerslev et al. 2001). Another unlabelled N source from the soil can be provided by ectomycorrhizal fungi (EM). EM lives in symbiosis with trees and thus provides host plants with the potential access to organic N and P (Marschner and Dell 1994). This could be important for the N supply, since wood ash treatment has been shown to increase (EM) in forest soil (Hagerberg and Wallander 2001).

The additional N supply, as suggested above for the A, W and LF treatment, was weakly reflected in an increase in N_{cont} and needle growth (see also Hallenbarter et al. 2002), in agreement with Egnell et al. (1998) for the A treatment. The ^{15}N recovery in the A and LF needles, however, was smaller compared to the control trees. This indicates an isotopic dilution effect for the A, W and LF treatment, due to an interchange between labelled N applied in all three treatments, and the non-labelled organic soil N (Nommik 1990). This indicates that a "priming effect" on microbial activity, inducing N mineralization, can be expected under increased irrigation (W) and fertilization (A and LF) as suggested by Ruppel and Makswitat (1999). Similar ^{15}N amounts 9 and 21 months after tracer application suggest, however, that N from previous-year needles (1999) was re-mobilized for the current-year foliage (2000), which is in agreement with the findings of Millard and Proe (1992).

The data presented here suggest that under the N-saturated conditions of this experiment, the wood ash treatment improved the N supply for spruce trees by affecting the microbial activity in the soil. The internal cycling of N seems to be reduced, which might have

implications especially in a mature forest stand, as Miller and Miller (1987) estimated the internal cycling to increase from 16% to 50% with increasing tree age (10–40 years) of *Pinus nigra* var. *maritima*. Thus in the A treatment, inorganic N sources from the soil became available and, therefore, the fertilizer effect on spruce trees was similar to the liquid fertilization treatment under the conditions of this experiment.

Acknowledgements This study, as part of the COST E6 and the HARWA project, was financed by the Swiss Federal Office of Education and Science (BBW) and by the Swiss Agency for the Environment, Forest and Landscape (BUWAL). Technical assistance was provided by K. Bleidissel and sample collections were made by P. Suter, T. Schmidlin, F. Hofmann and M. Fischer. The weather data were provided by MeteoSwiss.

References

- Ammann M, Siegwolf R, Pichlmayer F, Suter M, Saurer M, Brunold C (1999) Estimating the uptake of traffic-derived NO_2 from N–15 abundance in Norway spruce needles. *Oecologia* 118:124–131
- Birk EM, Vitousek PM (1986) Nitrogen availability and nitrogen use efficiency in loblolly pine stands. *Ecology* 67:69–79
- Bramryd T, Fransman B (1995) Silvicultural use of wood ashes—effects on the nutrient and heavy metal balance in a pine (*Pinus sylvestris*, L.) forest soil. *Water Air Soil Pollut* 85:1039–1044
- Buchmann N (1993) Wege und Umsetzungen von ^{15}N -Ammonium und ^{15}N -Nitrat in einem Fichtenjungbestand (*Picea abies* (L.) Karst.). Dissertation. Department of Plant Ecology, University of Bayreuth
- Buchmann N, Schulze ED, Gebauer G (1995) ^{15}N -ammonium and ^{15}N -nitrate uptake of a 15 year old *Picea abies* plantation. *Oecologia* 102:361–370
- Buchmann N, Gebauer G, Schulze E-D (1996) Partitioning of ^{15}N -labelled ammonium and nitrate among soil, litter, below- and above-ground biomass of trees and understorey in a 15-year-old *Picea abies* plantation. *Biogeochemistry* 33:1–23
- Bundt M, Widmer F, Pesaro M, Zeyer J, Blaser P (2001) Preferential flow paths: biological 'hot spots' in soils. *Soil Biol Biochem* 33:729–738
- Egnell G, Nohrstedt H-Ö, Weslien J, Westling O, Örlander G (1998) Miljökonsekvensbeskrivning (MKB) av skogsbränsleuttag, asktillförsel och övrig näringsskompensation (in Swedish). Forestry Board of Sweden, Jönköping
- Etiegni L, Campbell AG (1991) Physical and chemical characteristics of wood ash. *Bioresour Technol* 37:173–178
- Ferrier RC, Alexander IJ (1991) Internal redistribution of N in Sitka spruce seedling with partly droughted root systems. *For Sci* 37:860–870
- Fritze H, Smolander A, Levula T, Kitunen V, Mäkönen E (1994) Wood ash fertilization and fire treatments in a Scots pine forest stand, effects on the organic layer, microbial biomass, and microbial activity. *Biol Fertil Soils* 17:57–63
- Genenger M, Jaeggi M, Siegwolf R, Chalot M, Frossard E, Brunner I (2003a) Rapid ^{15}N uptake and metabolism in fine roots of Norway spruce. *Trees* 17:144–152
- Genenger M, Zimmermann S, Frossard E, Brunner I (2003b) The effects of fertiliser or wood ash on nitrate reductase activity in Norway spruce fine roots. *For Ecol Manage* 175:413–423
- Gessler A, Schneider S, Von Sengbusch D, Weber P, Hanemann U, Huber C, Rothe A, Kreutzer K, Rennenberg H (1998) Field and laboratory experiments on net uptake of nitrate and ammonium by the roots of spruce (*Picea abies*) and beech (*Fagus sylvatica*) trees. *New Phytol* 138:275–285

- Gundersen P (1998) Effects of enhanced nitrogen deposition in a spruce forest at Klosterhede, Denmark, examined by moderate NH_4NO_3 addition. *For Ecol Manage* 101:251–268
- Hagerberg D, Wallander H (2002) The impact of forest residue removal and wood ash amendment on the growth of the ectomycorrhizal external mycelium. *FEMS Microbiol Ecol* 39:139–146
- Hallenbarter D, Landolt W, Bucher JB, Schütz J-P (2002) Effects of wood ash and liquid fertilization on the nutritional status and growth of Norway spruce [*Picea abies* (L.) Karst.]. *Forstwiss Centralbl* 121:240–249
- Ingerslev M, Mälikönen E, Nilsen P, Nohrstedt H-Ö, Óskarsson H, Raulund-Rasmussen K (2001) Main findings and future challenges in forest nutritional research and management in the Nordic Countries. *Scand J For Res* 16:488–501
- Ingestad T, Aronsson A, Agren GI (1981) Nutrient flux density model of mineral nutrition in conifer ecosystems. *Stud For Suec* 160:61–71
- Jäggi M, Saurer M, Fuhrer J, Siegwolf R (2002) The relationship between the stable carbon isotope composition of needle bulk material, starch, and tree rings in spruce trees (*Picea abies*). *Oecologia* 131:325–332
- Linder S (1987) Responses to water and nutrients in coniferous ecosystems. In: Schulze E-D, Zwölfer H (eds) Potentials and limitations of ecosystem analysis. Ecological Series. Springer, Berlin Heidelberg New York, pp180–202
- Mälikönen E, Derome J, Fritze H, Helmisaari H-S, Kukkola M, Kytö M, Saarsalmi A, Salemaa M (1999) Compensatory fertilization of Scots pine stands polluted by heavy metals. *Nutr Cycl Agroecosyst* 55:239–268
- Marschner H, Dell B (1994) Nutrient uptake in mycorrhizal symbiosis. *Plant Soil* 159:89–102
- McDonald MA, Hawkins BJ, Prescott CE, Kimmins JP (1994) Growth and foliar nutrition of western red cedar fertilized with sewage sludge, pulp sludge, fish silage, and wood ash on northern Vancouver Island. *Can J For Res* 24:297–301
- Mead DJ, Pritchett WL (1975a) Fertilizer movement in a slash pine ecosystem. I. Uptake of N and P and N movement in the soil. *Plant Soil* 43:451–465
- Mead DJ, Pritchett WL (1975b) Fertilizer movement in a slash pine ecosystem II. N distribution after two growing seasons. *Plant Soil* 43:467–478
- Millard P (1994) Measurement of the remobilization of nitrogen for spring leaf growth of trees under field conditions. *Tree Physiol* 14:1049–1054
- Millard P (1996) Ecophysiology of the internal cycling of nitrogen for tree growth. *Z Pflanz Bodenkd* 159:1–10
- Millard P, Proe MF (1992) Storage and internal cycling of nitrogen in relation to seasonal growth of Sitka spruce. *Tree Physiol* 10:33–43
- Miller HG, Miller JD (1987) Nutritional requirements of Sitka spruce. *Proc R Soc Edinb* 93B:75–83
- Nambiar EKS, Bowen GD (1986) Uptake, distribution and retranslocation of nitrogen by *Pinus radiata* from ^{15}N -labelled fertilizer applied to podzolized sandy soil. *For Ecol Manage* 15:269–284
- Nambiar EKS, Fife DN (1991) Nutrient retranslocation in temperate conifers. *Tree Physiol* 9:185–207
- Nohrstedt HO (2001) Response of coniferous forest ecosystem on mineral soils to nutrient additions: a review of Swedish experiences. *Scand J For Res* 16:555–573
- Nommik H (1990) Application of ^{15}N as a tracer in studying fertiliser nitrogen transformations and recovery in coniferous ecosystems. In: Harrison AF, Ineson P, Heal OW (eds) Nutrient cycling in terrestrial ecosystems. Elsevier, London, pp 1–454
- Rennenberg H, Kreutzer K, Papen H, Weber P (1998) Consequences of high loads of nitrogen for spruce (*Picea abies*) and beech (*Fagus sylvatica*) forests. *New Phytol* 139:71–86
- Roberts DR, Toivonen P, McInnis SM (1991) Discrete proteins associated with overwintering of interior spruce and Douglas-fir seedlings. *Can J Bot* 69:437–441
- Ruppel S, Makswiat E (1999) Effect of nitrogen fertilization and irrigation on soil microbial activities and population dynamics—a field study. *Z Pflanz Bodenkd* 162:75–81
- Saarsalmi A, Mälikönen E (2001) Forest fertilization research in Finland: a literature review. *Scand J For Res* 16:514–535
- Schleppi P, Bucher-Wallin I, Siegwolf R, Saurer M, Muller N, Bucher JB (1999) Simulation of increased nitrogen deposition to a montane forest ecosystem: Partitioning of added ^{15}N . *Water Air Soil Pollut* 116:129–134
- Shepard RK (1997) Response of young black spruce [*Picea mariana* (Mill.) B.S.P.] to a mixture of wood ash and secondary papermill sludge. CFRU Progress Report 34. Maine Agric For Exp Stn Misc Rep 405:1–12
- Siegwolf RTW, Matyssek R, Saurer M, Maurer S, Schmutz P, Goerg-Günthardt M, Bucher JB (2001) Stable isotope analysis reveals differential effects of soil nitrogen and nitrogen dioxide on the water use efficiency of hybrid poplar leaves. *New Phytol* 149:233–246
- Wellburn AR (1998) Atmospheric nitrogenous compounds and ozone—is NO_x fixation by plants a possible solution? *New Phytol* 139:5–9
- Zhan G, Erich MS, Ohno T (1996) Release of trace elements from wood ash by nitric acid. *Water Air Soil Pollut* 88:297–311